17. A PROFUSION OF SPECIES? APPROACHES TOWARDS UNDERSTANDING THE DYNAMICS OF THE POPULATIONS OF THE MICRO-ARTHROPODS IN DECOMPOSER COMMUNITIES

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INTRODUCTION

The diversity of communities of soil micro-arthropods need not be reviewed: it has long been the subject of speculation at Congresses of Soil Zoology (e.g. Anderson 1975; Ghilarov 1977). One can, however, ask if the communities are unusually diverse, or if the diversity is an artefact of the way in which soil biologists view the communities. Several studies of the Collembola in the British Isles are shown in Figure 17.1, where it can be seen that no community, defined in terms of the dominant plant species, contained more than 25 species. Woodland communities tend to be more species-rich than grassland communities, which are richer than moorland communities. None of the data in Figure 17.1, which are restricted to insects in a single order, show a community that is particularly diverse. Indeed, Wood (1967) recorded a total of only 128 species of springtails and mites in a limestone grassland soil in Yorkshire, whereas Morris (1969, 1971) recorded more than 28 species of Heteroptera and 45 species of Auchenorhyncha in a chalk grassland habitat in Bedfordshire (these 73 species account for only part of the order Hemiptera). Comparisons, order by order, between the micro-arthropods of the soil and litter communities and the arthropods of the above-ground communities will probably indicate that the 'decomposer' communities are not as diverse as the 'grazer' communities. The habits of

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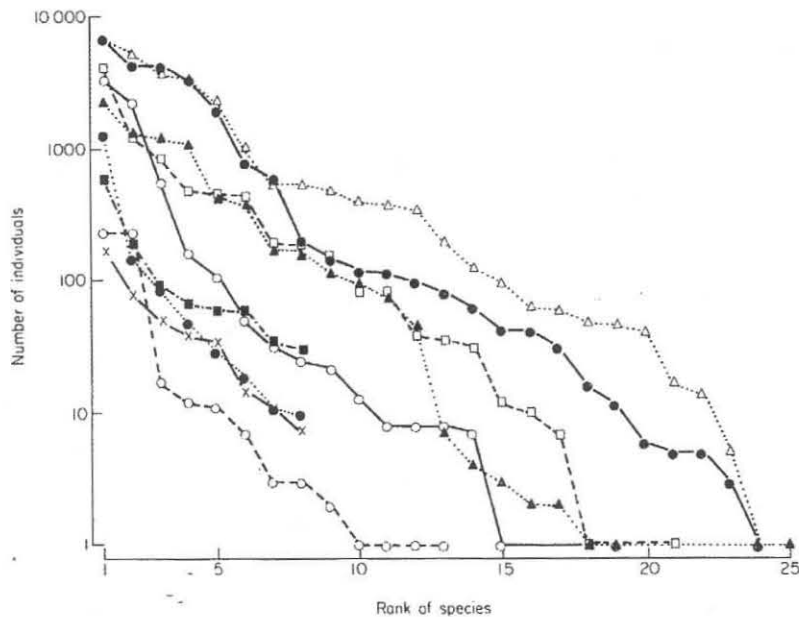
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FIG. 17.1.   Species abundance curves for Collembola in nine British habitats. From
right to left, approximately, the lines represent: a mixed coniferous forest (Poole
1961—dotted line, open triangles); Scots pine forest (Usher 1970—continuous line,
filled circles); various moorland habitats (Hale 1966)—alluvial grassland (dashed line,
open squares), limestone grassland (dotted line, filled triangles), *Calluna* (continuous
line, open circles) and *Juncus* (dashed line, open circles); and lowland habitats
(Macfadyen 1952) in which only the eight commonest species were recorded—*Molinia*
(dot and dash line, filled squares), *Deschampsia* (dotted line, filled circles) and *Juncus*
(continuous line, crosses).

ecologists looking at only one order and of soil biologists looking at all orders
have almost certainly led to an erroneous belief in an unusually diverse
decomposer community. Soil and litter communities usually contain less than
150 micro-arthropod species within any habitat defined in terms of a reasonably
homogeneous area of vegetation.

Generally, two fundamentally different approaches have been used to
investigate the structure and functioning of communities. To borrow terms
from the field of numerical classification, these could be called 'divisive' and
'agglomerative'. The divisive approach consists of sampling a community, and
analysing the results in order to pick out temporal, spatial and other patterns
and correlations. In other words, the unit of study is the community and the
aim is the analysis of patterns of individual species within it. The agglomerative
approach consists of taking individual species of a community and studying

their biology, and their paired and higher-order interactions. The unit of study is thus the species, and the aim is to build predictive models of successively more and more complex artificial communities. Both approaches are reviewed in the following sections, and results are given from some of our studies, either in the Black Wood of Rannoch, Perthshire (divisive studies), or in the grasslands on the Yorkshire Wolds (agglomerative studies).

THE DIVISIVE APPROACH

The aim of the divisive approach is to find patterns of species within samples drawn from the whole community. These patterns range from traditional ecological investigations, such as the seasonal, vertical and horizontal distribution of individual species, to multivariate studies which relate species distributions to the environmental influences. Following the ideas of Hutchinson (1957) and the work of MacArthur & Levins (1967), it seems possible that multivariate analyses might also yield information on the niches occupied by the individual species, and on the extent of niche overlap.

Seasonal distribution

The seasonal distribution, or phenology, of the species of soil micro-arthropods has been described by many authors: Hale (1967) and Wallwork (1967) have reviewed the literature relating to Collembola and mites respectively. Many of the studies of seasonal distribution can be criticized for their short duration. Most studies span merely a single year (such as those of Usher 1970, 1971b, 1975b or Niijima 1971 on Collembola) or a period only slightly in excess of a year (such as those of Moritz 1963 and Lions 1973 on Cryptostigmata populations). Hale's (1966) study of moorland Collembola spanned two years, but only studies like Tamura's (1976) of *Folsomia octoculata* for three-and-a-half years and van der Drift's (1959) of various beetles for six years provide data which can be analysed to estimate both the true seasonal distribution and the year-to-year variation. Descriptive studies of individual species yield little information that can be interpreted in terms of community structure, and it appears that a study of the phenology of a whole soil arthropod community has not been attempted.

The data used by Usher (1970, 1971b, 1975b) have been reworked and are shown in Figure 17.2. The illustration shows the total number of Collembola, Mesostigmata and Cryptostigmata (and the five most abundant species in each group) in 1 536 cm³ of Scots pine litter sampled at twelve times during one year. Some of the statistics for comparison of these graphs are listed in Table 17.1.
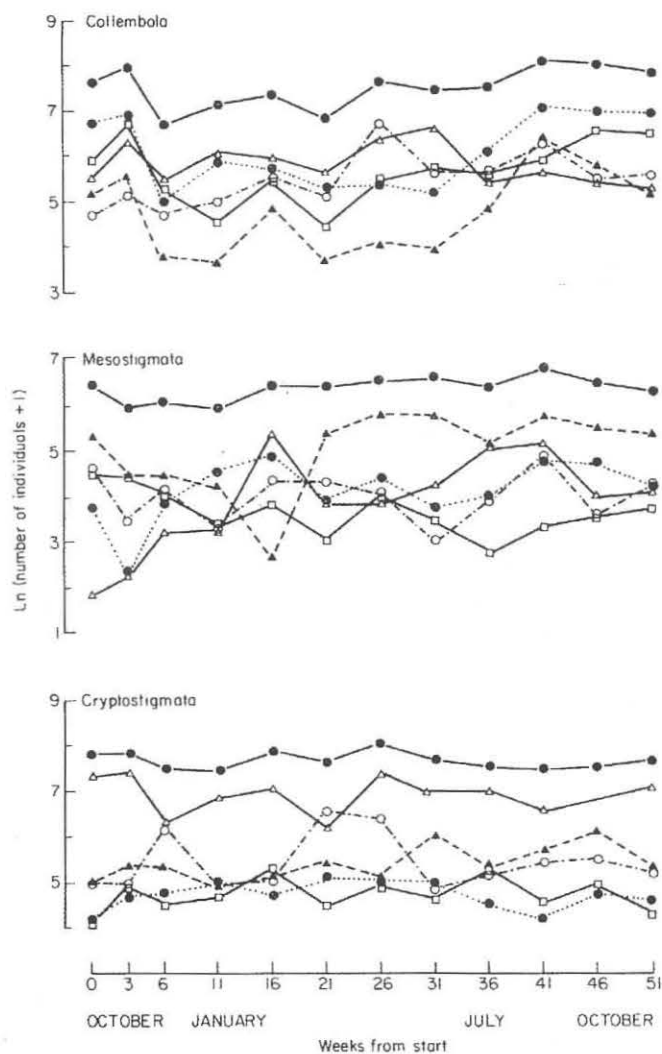
FIG. 17.2. Seasonal variability in populations and communities of soil arthropods (data from Usher 1970, 1971b, 1975b). The upper set of lines represent the Collembola, the centre the Mesostigmata and the lower the Cryptostigmata. In each case the total count for that group (continuous thick line joining filled circles) is shown together with the five most abundant species in the group. The species codes (shown in Table 17.1) respectively for the three groups are: dotted line, filled circles (Oa, Vn, Ap); continuous line, open squares (Fm, Pl, Cb); continuous line, open triangles (Is, Pr, Tv); dashed line, filled triangles (Tc, Om, Sm); and dot and dash line, open circles (Fq, Tp, Pp).

TABLE 17.1. The mean (*m*), the coefficient of variation (*CV*) and code (used in Figures 17.2, 17.4 and 17.5) of the total of all Collembola species, all Mesostigmata and all Cryptostigmata, as well as the five most frequent species in each group, in twelve samples of 1 536 cm^3 of Scots pine forest litter and humus. All data have been transformed by ln ($x + 1$) before analysis, and no back-transformation has been carried out. The 'maximum *CV*' for the three totals represents what the *CV* would have been if all of the species in the group had been synchronous, i.e. that the rank correlations between all pairs were 1

Group/species	Code	*m*	*CV* (%)	Maximum *CV* (%)
Total Collembola	—	7·49	6·1	9·2
Onychiurus absoloni	Oa	6·12	13·9	
Isotoma sensibilis	Is	5·80	7·2	
Friesea mirabilis	Fm	5·67	12·6	
Folsomia quadrioculata	Fq	5·46	11·0	
Tullbergia callipygos	Tc	4·73	19·5	
Total Cryptostigmata	—	7·76	2·5	6·4
Tectocepheus velatus	Tv	6·83	6·6	
Platynothrus peltifer	Pp	5·42	11·2	
Steganacarus magnus	Sm	5·39	6·8	
Ceratoppia bipilis	Cb	4·70	8·2	
Adoristes poppei	Ap	4·70	6·1	
Total Mesostigmata	—	6·36	4·4	11·9
Olodiscus minimus	Om	4·97	18·3	
Veigaia nemorensis	Vn	4·17	17·2	
Trachytes pyriformis	Tp	3·98	13·9	
Parazercon radiatus	Pr	3·84	28·3	
Pergamasus lapponicus	Pl	3·64	13·5	

The total community of Cryptostigmata remains remarkably constant throughout the year, since the individual species tend to complement each other. Similar results can be seen for the Mesostigmata, where the coefficient of variation for the whole community is less than those for the five most abundant species. The fact that the individual species of mites are not at their most abundant at the same time of the year invites speculation that this is the result of either extant interspecific competition or temporal separation evolved to avoid it.

The situation in the Collembola is different. Many authors have referred to a pattern of autumnal maximum and vernal minimum in collembolan population sizes. This is seen in Figure 17.2, where there is a considerable degree of synchrony between the five most abundant species. Why the mite species appear to be asynchronous and the Collembola species to be synchronous is a question that cannot yet be answered. An answer will probably lie in the generality or specificity of the feeding habits of the different groups.

Vertical distribution

Reviews of the vertical distribution of species of Collembola are given by
Christiansen (1964) and Hale (1967), and of mites by Wallwork (1967). These
reviews indicate two basic approaches to the study of vertical distribution. In
one approach the measurement of depth is absolute: for example, Athias
(1975), working on a West African savannah soil, divided the soil into 0–15 cm
and 15–40 cm depths, and Usher (1970, 1971b, 1975b) used three slices, each
1 cm thick. In the other approach, depth is relative to the horizons of the soil
profile; thus, Poole (1961) recorded Collembola in the litter, humus and sub-
humus horizons, and Hurlbutt (1964) observed *Veigaia* mites in the litter and
fermentation, humus and a_1 horizons.

Again using the data discussed by Usher (1970, 1971b, 1975b), a mean
annual depth, weighted by population size, has been calculated for the five
most abundant species in each of three arthropod groups (Fig. 17.3). The
Collembola are well spaced out on the depth axis, except for *Friesea mirabilis*
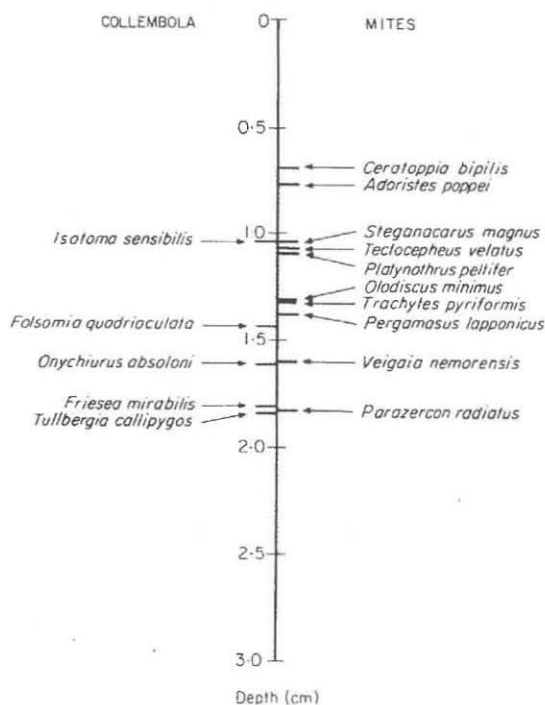

Depth (cm)

FIG. 17.3. The weighted average annual mean depth of the fifteen species of soil
arthropods shown in Figure 17.2. The data are reworked from Usher (1970, 1971b, 1975b).

and *Tullbergia callipygos*, which are unlikely to compete for food since *F. mira-bilis* has mouth parts adapted for sucking whilst *T. callipygos* will ingest solid food which it is able to grind. The mites tend to cluster rather more on the vertical axis. All the Cryptostigmata species occur near the surface of the soil, while all the Mesostigmata species are deeper. However, the inadequacy of the sort of data shown in Figure 17.3 is clear for two reasons. First, the method of sampling in 1-cm slices, although thinner than used in most studies of the vertical distribution, is still far too crude, and it can at best only give a rough approximation to the vertical distribution. Secondly, since the arthropods are likely to be associated with particular stages in the decomposition of dead plant material, it is uncertain whether the observed distribution reflects the vertical distribution of the decomposition process and hence of potential food, or the vertical distribution of the species reaction to environmental gradients.

Many of these problems have been overcome by adopting a radically different sampling process (Anderson 1971; Pande & Berthet 1975) in which thin sections of the organic horizon of the soil are cut. The vertical distribution of the species can thus be related both to depth and to the stage of decomposition. Pande and Berthet's study of Cryptostigmata, in 40 horizontal slices of the surface 6 cm of the soil, clearly shows that there is a spatial separation of the species. The depth in the soil is thus likely to be another factor which can be exploited by the species of the soil micro-arthropod community to avoid inter-specific competition.

Horizontal distribution

Soil biologists have been fascinated by the aggregated nature of the distribution of soil arthropods, and many studies have been directed solely at demon-strating this form of distribution (reviewed by Christiansen 1964 and Butcher, Snider & Snider 1971). Controversy raged as to whether the distribution was nearer the negative binomial, the Neyman type A, or some other form (for example, Hartenstein 1961); but, with hindsight, it seems that three important features of the aggregated distribution were, at least initially, overlooked.

First, why did the arthropods aggregate where they were observed? Reviewing the literature, Usher (1976) concluded that the location of food and the local conditions of moisture were the two most likely stimuli. Studies by Joosse (1970) have indicated that there may be social reasons for aggregating behaviour: in animals with no courtship, or direct sperm transfer, aggregation brings the two sexes into contact, increasing the probability of fertilization. It has been speculated by Joosse & Verhoef (1974) that the aggregated distribu-tion has an important survival value during the moult. This will be particularly effective if the arthropods are able jointly to provide a defence mechanism against predators. Laboratory studies, as indicated later, suggest that *Hypogastrura* might gain protection by aggregating to moult (Strebel 1932). It seems

less likely that species in family Isotomidae, Entomobryidae or Sminthuridae (*sensu* Gisin 1960) could gain protection in this way, although the warning of a predator's proximity afforded by an attack on one invididual may have a survival value to the remainder. The recent detection by Verhoef, Nagelkerke & Joosse (1977) of an aggregation pheromone is of considerable importance, especially if the pheromone causes a species to aggregate and predators to avoid that aggregation.

Secondly, is there any kind of relation between aggregation behaviour and population density? Usher (1969, 1971a, 1975a) attempted to investigate this question by recognizing three distinct kinds of relations, which are outlined in Table 17.2. Using the commoner species shown in Figures 17.2 and 17.3, most of the Collembola and some of the Mesostigmata showed a type I response, whereas the Cryptostigmata showed either a type II or type III response. As a population increases, the Collembola and Mesostigmata are able to found new aggregations, while the Cryptostigmata increased the size of their aggregations. These observations suggest that the Collembola have wider niches, and are therefore able to establish new foci for aggregations, while the Cryptostigmata have narrower niches, and therefore increase their population density within an existing aggregation.

Thirdly, is an aggregation a single-species or a multi-species phenomenon? Attempts to compare indices based on the variances of numbers of the single species with the index of all species pooled together are unconvincing, though they have been used to suggest that aggregations are multi-specific (e.g. Poole 1961). Soil cores are probably far too insensitive to allow for a detailed study of whether several species can join together in an aggregation, although the new techniques of soil sectioning probably offer the best chance of investigating this aspect of soil micro-arthropod communities. If aggregations are found to be multi-specific, one will need to ask if and how the species avoid competition

TABLE 17.2. r_n is defined as the correlation between population density and the number of aggregations per unit of soil volume; r_s as the correlation between density and the mean number of organisms per aggregation. Depending on the significance or non-significance of r_n and r_s, the table defines three types of aggregation behaviour, designated I, II and III, with possible variants on each of these basic types (designated I?, etc.). A further three of the cells are unlikely to occur (designated --)

		r_n	
r_s	Positive	Non-significant	Negative
Positive	III	II	II?
Non-significant	I	III?	--
Negative	I?	--	--

within the aggregation, and whether the chemical defences of one species are used by other species to gain protection against predators.

Multivariate analyses—an indication of the niche?

One early empirical attempt to relate micro-arthropod distribution to the environment was that of Haarløv (1960), though Poole (1961) carried out a more extensive analysis using correlation and partial correlation coefficients. Due to the correlation between the environmental variables measured, such attempts have generally proved relatively unsuccessful. Curry's (1973, 1976) studies take the analysis of the relation between soil arthropods and their environment further, by comparing the mean numbers of arthropods occurring beneath different plants, and then using a principal components analysis to identify associations.

One should ask what a principal components or principal co-ordinates analysis is likely to reveal. If a set of samples or observations (species, environmental variables, or both) are ordinated on the principal axes accounting for the greatest variance, then the existence of clusters will indicate communities or associations. If the axes have meaning as resources when the samples drawn from a single cluster or association are analysed, then the location of a species on the diagram gives an indication of its niche in relation to those resources. This approach has been attempted by a principal component analysis of the data for the fifteen species of soil micro-arthropods shown in Figures 17.2 and 17.3. Since the 1 119 samples were taken over a period of one year, they have been divided into three approximately equally sized groups representing the cold period of the year (November to February) and periods of increasing (March to July) and decreasing (August to October) temperature. Having transformed the data by ln $(x + 1)$, the results of these three analyses, plotted on the same ordination diagram, are shown in Figure 17.4. If the principal axes represent the niches of the species in some abstract manner, a triangle formed by the three analyses could be considered to approximate the area of the niche space occupied by a species. In general, there is remarkably little overlap of the triangles, except for that of *Isotoma sensibilis* which overlaps three of the Cryptostigmata species. The spacing of the species on this diagram suggests that there is some separation of their niches.

However, to understand these niches, the principal axes would need to be identified with a measurable property of the ecosystem. Comparison of the first axis with the depth diagram in Figure 17.3 indicates that species with a small mean depth tend to be at the left of the illustration. No interpretation of the second principal axis can be offered. Depth was a factor included in the sampling since one-third of the samples were taken from each of three layers. To eliminate depth the three counts were added together to give a 'core count', which, after transformation, was analysed (Fig. 17.5). The first two principal
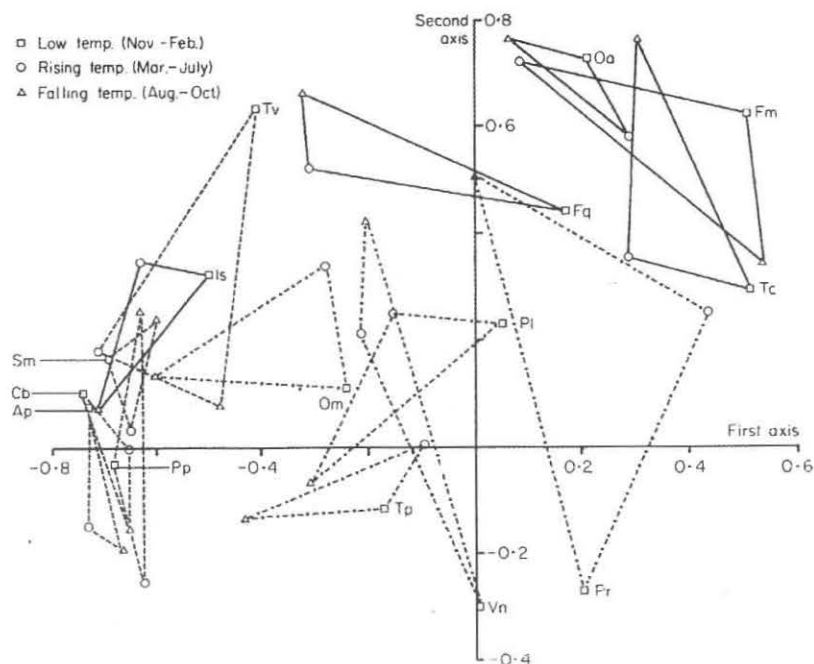
FIG. 17.4.   A plot of the first two axes of principal component analyses of the fifteen
species (Table 17.1) in 1 119 samples, divided into three groups depending upon the
temperature. The positions of a species in the three analyses are joined by a triangle,
continuous lines representing Collembola, dashed lines Cryptostigmata and dotted
and dashed lines Mesostigmata.

axes are now not interpretable in terms of known environmental variables,
though the third axis tends to correlate with depth. The species in Figure 17.5
are all well separated, indicating their niche separation in relation to these
abstract axes.

These analyses, in which the principal axes cannot be identified, are certainly
less satisfactory than that of Miracle (1974), who was able to identify her axes.
She found that her first three axes accounted for 58% of the variance, whereas in
Figure 17.4 the first three axes account for only 45%. It is possible that soil
biologists, whose history of studying communities is shorter than that of
aquatic biologists, have not yet identified some of the environmental influences
acting upon soil arthropod populations. It is also possible, and perhaps more
likely, that multivariate analyses are not going to shed any light upon the niche
structure of communities. Maxwell (1977) indicates that in the behavioural
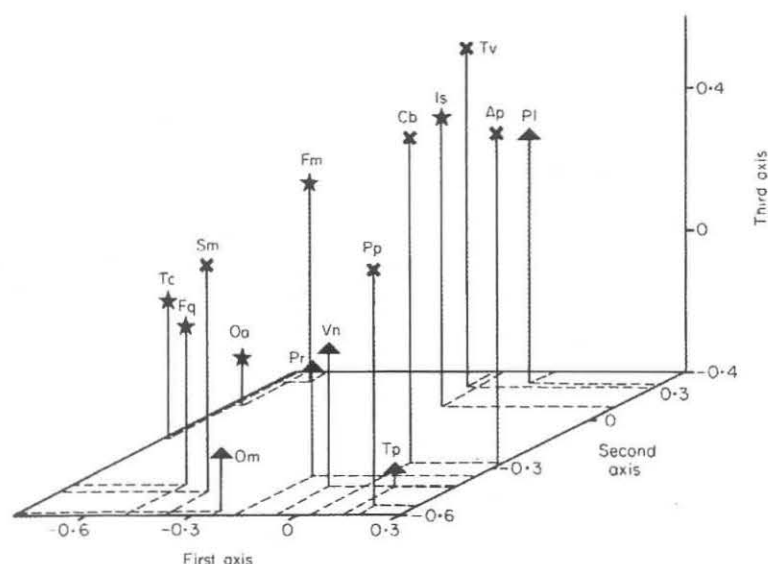sciences there were great expectations of multivariate techniques which have, in

FIG. 17.5. Principal components analysis of the complete data shown in Figure 17.4, but summed so that cores are analysed rather than series of samples taken at three different depths. Stars, crosses and triangles represent Collembola, Cryptostigmata and Mesostigmata respectively.

general, not been realized due to the low level of correlation existing between different categories of 'tests'. The problem of extremely small correlation frequently occurs in ecological data.

THE AGGLOMERATIVE APPROACH

Immediately one thinks of investigating the dynamics of single-species populations, or two species interacting, the problem of applying the experimental findings needs to be considered. Experiments are usually carried out in the laboratory, where the diurnal temperature cycle has a smaller amplitude than that in the field, and other environmental variables are kept more or less constant. The environment of laboratory cultures is considerably more predictable than that of field populations. Since the soil environment is buffered against extremes of temperature, there is the small consolation that laboratory conditions more closely approach soil conditions than above-ground conditions. Also, soil provides the arthropods with an opaque three-dimensional environment which, if it is recreated in a laboratory, presents the experimenter with problems both of taking a census and of observation. The majority of

laboratory studies have reduced the environment to an approximately flat surface, and therefore density cannot be easily compared between populations in cultures and populations in soil.

Studies of single species

The simplest way to investigate the dynamics of single species is to maintain cultures in the laboratory; this has yielded information on the relation between fecundity and density (Green 1964; Usher & Stoneman 1977), mortality (Usher & Stoneman 1977), inhibition of oviposition and oophagy (Waldorf 1971a,b) and life history, speed of development, duration and number of instars, etc. (these have been reviewed by Butcher, Snider & Snider 1971). Another class of techniques relies on field observations or on inference based on field samples. Thus, after nine seasons of field work, Wallace (1967) was able to demonstrate the nature of the control of populations of *Sminthurus viridis* by environmental factors, by a predatory mite and by a density-dependent factor (eating of apparently toxic bodies of dead individuals by early instar insects). Studies by Lebrun (1970) and Joosse (1969) have inferred such population parameters as fecundity, mortality and speed of development, quoting their results as yearly averages or on a seasonal basis. The dilemma facing anyone experimenting with single-species populations is that field studies relate the population parameters to the seasonal cycle in the environment, whereas laboratory studies relate these parameters to the density of the animals; there seems to be no satisfactory method of relating the population parameters both to seasonality and to density.

Another aspect of laboratory studies that is of relevance to community ecology is the productivity of an exploited population and the exploitation that can be tolerated before the species is ruinously heavily exploited. Experiments described by Usher, Longstaff & Southall (1971) on *Folsomia candida* distinguish numerical production of a population from biomass production. Although there were no significant differences between the numerical productions of cultures with excess food in which 30%, 40%, 50% and 60% of the population were removed every 14 days, biomass production was at a maximum when exploitation was 30%. More detailed investigations of *Onychiurus armatus* (*s. lat.*) by Costigan (1975) indicate that a maximum numerical production occurred when between 40% and 60% of the population was removed every 18 days (a model of his experimental system indicated the actual maximum at 48%). These laboratory experiments show that the Collembola can produce large numbers of offspring in the presence of continued predation, though it is unlikely that field population densities approach those of laboratory cultures when production is reduced by intraspecific competition. Whether it is important to consider biomass production (heavily weighted in favour of large individuals) or numerical production (heavily weighted in favour of young,

newly emerged individuals) when considering the effects of predators in a natural community is unknown.

Competition between species

Studies of the competitive relations between species of soil arthropods are rare, though more is understood about phytophagous mites (see Huffaker, Vrie & McMurtry 1969). Christiansen (1967) investigated only 13 of the possible 55 pairwise interactions between the 11 species of Collembola that he had available; in only one of his experiments, that of *Sinella coeca* with *S. curviseta*, did he get an indication of long-term co-existence. Inference based on field sampling of *Veigaia* and *Asca* mites has been attempted by Hurlbutt (1968), who suggested that species of moderately high anatomical similarity are more likely to co-exist than species that are either extremely similar or of low similarity. This concept of similarity seems not to have been widely used in ecology; its problem in application lies in the finding of a satisfactory measure of similarity that can be used in many groups. The observation presumably reflects a compromise between character divergence in co-existing generalist species (Lawlor & Maynard Smith 1976) and the constraints imposed by a common environment.

Longstaff (1974) investigated both intra- and inter-specific competition in three species of Collembola, *Hypogastrura denticulata*, *Onychiurus armatus* (*s. lat.*) and *Sinella coeca*, and constructed models of the system (Longstaff 1977). Full details of the culturing and census techniques are given by Longstaff (1974). At laboratory temperature (mean 23°C, range 15–30°C) there was no evidence of co-existence between species. In competition with either *S. coeca* or *O. armatus*, *H. denticulata* usually had become extinct before the end of the 24-week experimental period, irrespective of its initial proportion. *O. armatus* was always eliminated from cultures with *S. coeca*. Of the 36 cultures, only four still had both species surviving together after 24 weeks (these were all cultures of *O. armatus* and *H. denticulata* initiated with equal numbers of the two species or with excess of *H. denticulata*).

In contrast, at a constant temperature of 16°C, *H. denticulata*, in competition with *O. armatus*, always either remained or became the dominant species, though *O. armatus* never become extinct. In cultures with *S. coeca*, *H. denticulata* similarly increased its population size, though numerical dominance appeared to be retained by the species in the greatest abundance in the initiating culture. At this temperature it appears that *H. denticulata* is able to co-exist with either of the other species. *O. armatus*, although persisting with *H. denticulata*, usually became extinct in cultures with *S. coeca*. The fecundity of *O. armatus* was initially increased above the level in single-species cultures by the presence of *H. denticulata*, though in the presence of *S. coeca* the fecundity was either reduced or the animals failed to breed. *S. coeca* populations

were apparently unaffected by the presence of *O. armatus*. Of the 36 cultures maintained at 16°C, only in nine of them had one or other species become extinct within 24 weeks. In relation to field conditions, this result could indicate either that it takes longer for competitive exclusion to occur at lower temperatures or that soil arthropods are more able to co-exist at temperatures more similar to, though still higher than, those in their natural environment. That few of the populations at 16°C declined supports the latter hypothesis, though it leaves unanswered the question of what mechanism allows co-existence.

Longstaff's experiments are summarized in Figure 17.6, in which the total productivity (area under the population size curve and hence in units of 'insect weeks') of the different species is compared. If competition is defined as occurring when two or more species all experience depressed fitness due to their mutual presence together (Emlen 1973), Figure 17.6 indicates that there is little genuine competition. At laboratory temperatures only one species of any pair showed a depressed productivity in the presence of the other and hence these interactions are probably best termed amensalism (cf. Longstaff 1976). At 16°C
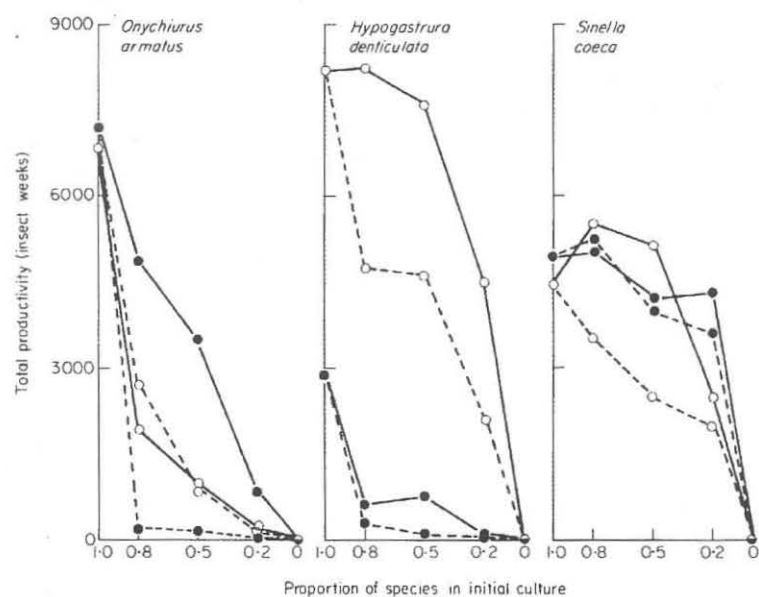

FIG. 17.6.   Summaries of the results of competition (Longstaff 1976) by replacement series diagrams. Open and filled circles indicate cultures at 16°C and in the fluctuating laboratory environment respectively. On the *O. armatus* diagram the continuous and dashed lines indicate performance of the species in the presence of *H. denticulata* and *S. coeca*; on the *H. denticulata* diagram the lines represent the presence of *O. armatus* and *S. coeca*; and on the *S. coeca* diagram the lines represent the presence of *O. armatus* and *H. denticulata*, all respectively.

two of the interactions resulted in the depression of the productivity of only one species, while the interaction between *H. denticulata* and *S. coeca* depressed neither species and hence is likely to lead to long-term co-existence of both species.

Without identifying the mechanisms of competition/amensalism, and with totally unpredictable interactions such as the increased fecundity of *O. armatus* in the presence of *H. denticulata*, Longstaff was unable to predict the outcome of the three species interactions from the data he had collected from single-species populations and all their pairwise interactions.

Predation by one species on another

Many groups of animals in the soil ecosystem have been identified as predators: spiders, beetles (especially Carabidae, Staphylinidae), pseudo-scorpions and mites (particularly the Mesostigmata). Whilst predators in all these groups (e.g. Christiansen 1971) will feed on the soil micro-arthropods, there is increasing evidence that the predatory mites exert the largest predatory influence on the species of soil micro-arthropods (e.g. the review by Huffaker, Vrie & McMurtry (1969) for the control of phytophagous mites and Wallace's (1967) study of the control of *Sminthurus viridis*). The importance of predation is indicated by the occurrence of defence and escape mechanisms in the potential prey. Collembola occurring in the litter layer have a well-developed jumping apparatus, the furcula, whilst those deeper in the soil appear to have a chemical defence mechanism which is at least partially effective in deterring predators (Usher & Balogun 1966).

Harris (1974b) studied the feeding of one species of mite, *Pergamasus longicornis*, on three species of Collembola and demonstrated that most of the life-history phenomena were dependent upon the population density of their prey. The time taken to find and capture a prey is dependent upon the density of prey for both juvenile (Fig. 17.7a) and adult mites (Fig. 17.7b). The sexes have different capture rates when the mites are juvenile at which stage the sexes are superficially identical, whereas when the mites are adult (and can be sexed by eye) the capture rates are more closely similar (regression lines are shown in Figs 17.7a,b). The speed with which the mites developed from larva to adult in a constant temperature of 20°C is linearly related to the rate with which prey were caught (Fig. 17.7c). Although the females capture prey quicker than males, there is no difference between the sexes in the relation of development time to capture rate. The implication of the regression line in Figure 17.7c,

$$D = 10.3 + 18.2t$$

where D is the development time and t is the time per capture in days, is that there is an upper ceiling to a mite's development rate, and that the slower the mite develops the less total prey it needs to catch for development to adulthood.
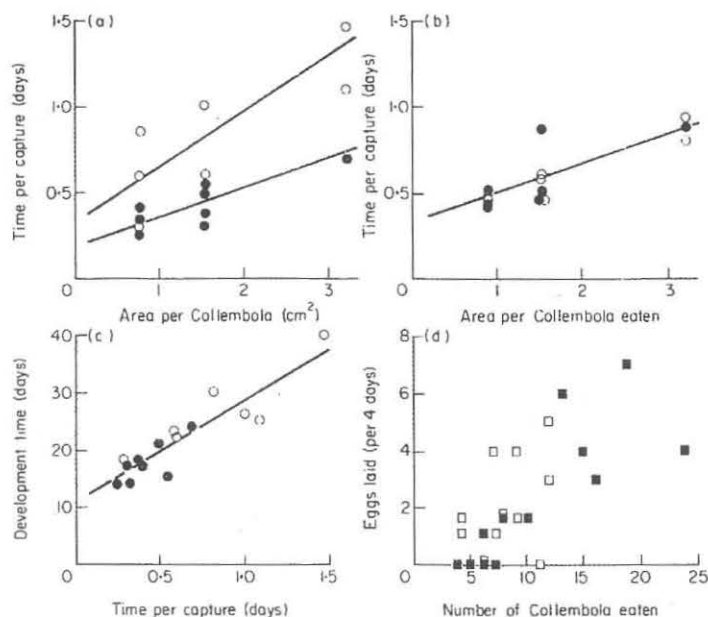
FIG. 17.7.   (a) The relation between time per capture by *Pergamasus longicornis* and prey (*Folsomia fimetaria*) density over the period from the predator hatching from an egg till the final moult (Harris 1974b). (b) Similar data for adult *P. longicornis*. (c) The relation between the total development time of *P. longicornis* and the time required to capture and handle one prey individual. In these three diagrams open and filled circles represent males and females respectively. (d) The relation between the number of eggs laid per 4 days and the number of prey eaten by female *P. longicornis*. Open and closed squares indicate maximum prey densities of 0·65 and 1·30 *F. fimetaria* cm⁻² respectively.

The decrease in the number of prey required for development as t increases is contrary to what might be expected if maintenance of the mite took a significant proportion of the food it consumed. Similarly, there appears to be some upper asymptote to the relation between the number of eggs laid and the rate of ingestion of prey, though there is considerable variation in these data (Fig. 17.7d).

An interesting feature of *P. longicornis* is the variety of its effective functional responses. A least squares fit of an integrated version of the Holling disc equation (Harris 1974a) to the observed consumption of *F. fimetaria*, *H. denticulata* and *S. coeca* yielded the curves shown in Figure 17.8. The ranges of prey densities depicted probably span those encountered by the mite in the field (Harris 1974b). The type of the functional response in this predator clearly depends upon the prey on which it is feeding. When feeding on *F. fimetaria*, there is a typical type II response by both male and female mites, whilst both
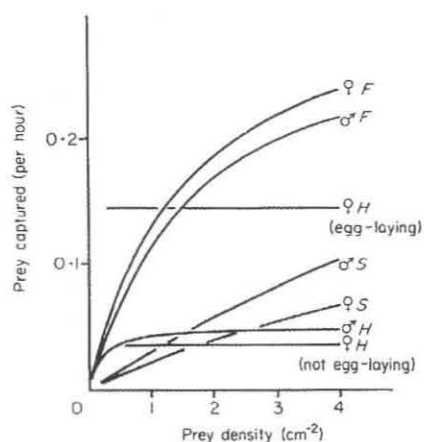
Fig. 17.8. The functional response of *P. longicornis* to prey density, the experimental data being smoothed by Harris' (1974a) model. The symbols indicate first the sex of the mite and second the prey species: *F*, *S* and *H* representing *F. fimetaria*, *S. coeca* and *H. denticulata* respectively. Female mites preying upon *H. denticulata* are divided into two sets according to whether or not they laid eggs.

sexes seem to show a linear response, without a plateau being reached, when feeding on *S. coeca*. Predation by either sex upon *H. denticulata* is effectively independent of prey density, the rise towards the plateau presumably occurring on lower densities than those included in the experiment. These results led Harris & Usher (1978) to speculate that, under predation by *P. longicornis*, populations of *S. coeca* are likely to be more stable than those of *F. fimetaria*, whilst populations of *H. denticulata* are likely to be very unstable. This expectation seems to be in accord with reported observations of swarming in the Collembola.

Predation by one species on more than one other

Davis (1978) investigated predation upon two species of Collembola, *Hypogastrura denticulata* and *Sinella coeca*, at a constant temperature of 16°C. As *Pergamasus longicornis* had displayed excessive cannibalism under Harris' culture conditions, it was replaced by another predatory Mesostigmatid mite, *Hypoaspis aculeifer*. Cultures were set up to investigate each pairwise interaction between the three species, and the results were used to construct a three-species population model. The predictions of this model were compared with data gained from an experiment conducted over a nine-month period in which 56 different initial conditions, representing different proportions of the two-prey species and the life-history stages of the mite, were investigated.
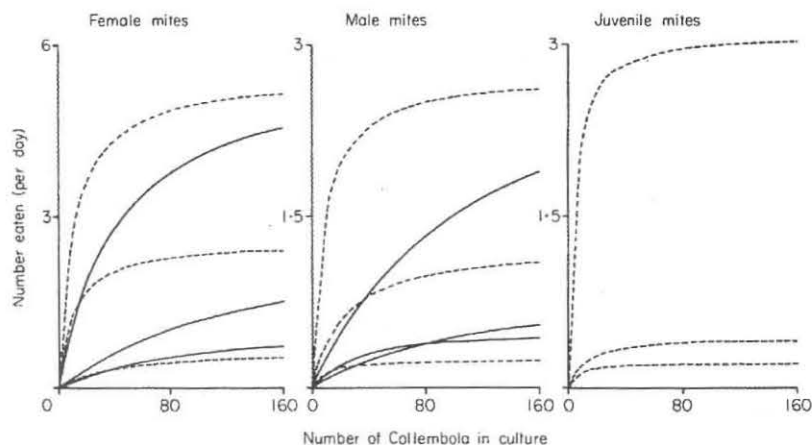
FIG. 17.9. Predation by *Hypoaspis aculeifer* (separated into male, female and juvenile) upon *S. coeca* (continuous lines) and *H. denticulata* (dashed line). In each illustration the upper curve represents predation on small prey, the centre curve on medium-sized prey and the lower curve on large prey. Since juvenile mites were largely unable to catch *S. coeca*, that family of curves has been omitted from the diagram. The curves were derived by Davis (1978).

In the presence of a single-prey species, *H. aculeifer* always displayed a type II response when preying upon one size class of either *S. coeca* or *H. denti-culata* (see Fig. 17.9). Whilst the number of eggs laid was linearly related to an approximate measure of the biomass (the cube of the length of the size class concerned) of *S. coeca* eaten, *H. aculeifer* could hardly reproduce on a diet of only *H. denticulata*. When both species were present, maximum daily fecundity was in excess of that which could be expected from the amount of *S. coeca* eaten, and so it would appear that a diet of *H. denticulata* is deficient in some manner and that the presence of *S. coeca* in the diet overcomes this deficiency (Table 17.3). If such interactions between prey species in their effect upon the

TABLE 17.3. The fecundity of *Hypoaspis aculeifer* when feeding upon *Sinella coeca*, *Hypogastrura denticulata*, and both species in mixed culture. In all three experiments there were 40 prey individuals in the culture

Prey	Number of females	Eggs per female (over a 12-day period)	Maximum number of eggs per female per day
40 *S. coeca*	18	7·72	2
40 *H. denticulata*	18	0·67	1
20 of each species	27	7·19	4

predator are common, the aim of the agglomerative approach to build simple studies into complex community studies will be impossible to achieve.

Davis found that *H. aculeifer* females, when offered a choice of prey, displayed switching only when they had been starved. The data were gained from a 12-day experiment, before which the predators were starved for one day, during which counts were made every four days. A significantly higher level of predation was recorded in the first four-day period, during which significant switching occurred towards the preferred prey species, *S. coeca* (using an assumption of a random predator, the observed kill of *S. coeca* was 6·67 individuals above that predicted by the model, whilst the kill of *H. denticulata* was only 0·41 above the prediction; for individuals in the second two four-day periods the figures were 1·01 and 0·94 respectively). The experiments also indicated that there was a significant amount of switching to the smaller size classes of *S. coeca* only during the first four-day period. There was no evidence of switching between size classes when *H. denticulata* was the only prey species. These results contrast to the predictions of the optimum feeding theory (MacArthur & Pianka 1966) and the findings of Ernsting (1977). It is possible that the results for *H. aculeifer* are due to increased activity of starved predators disturbing the more mobile prey species or the more mobile size class of the species, in which case the switching would be a reflection only of the physical interactions which occur in the simple experimental culture and which may not occur in the field. It is possible that *H. aculeifer*, operating in an environment in which food is scarce, and hence also hungry, would not exhibit switching.

Without the inclusion of switching, Davis' predation model always predicted a disturbance of co-existence at densities at which co-existence was to be expected, and an increase in the speed of competitive exclusion when that was the most likely result of the interaction between two prey species in the absence of predation. The results of the experimental cultures were variable (see Davis 1978), but the model's predictions were borne out in all but one of the 56 cultures assessed. It is possible that predators in the soil will experience a much lower density of prey than in culture, and it might therefore be predicted that predators would be hungry more frequently. Also, a diurnal rhythm of temperature and light may well tend to produce hungry predators at various times of the day. If switching by *H. aculeifer* occurs in the field it may result in opposite conclusions with respect to the co-existence of prey species. Although the requirement of simplicity has forced stenophagy upon the majority of predators used in laboratory studies, there is little or no evidence that species of predatory mites are stenophagous in the soil ecosystem and certainly none to refute the belief that the generalist predator is the more common.

A further observation is that *H. aculeifer* populations persisted longer in the total absence of prey than in the presence of only *H. denticulata* and, similarly, juvenile *P. longicornis* suffered a high mortality when feeding on this species (Harris 1974b). *H. denticulata* thus appears to be toxic to these predatory mites.

This may be interpreted as an evolutionary response to its life deeper in the soil than *S. coeca*, where it is less able to avoid predation by jumping.

Environmental heterogeneity

The well-known experiments of Huffaker (1958) indicated that the persistence of simple communities of predatory and non-predatory mites was dependent upon the heterogeneity of the environment in which they live. However, there has been virtually no consideration of this factor in laboratory studies of the soil micro-arthropods. Culver (1974) introduced patchiness into his laboratory cultures, in which, over a 68-day period, *Folsomia candida* and *Lepidocyrtus cinereus* co-existed. However, due to the experimental design one cannot state whether co-existence is a phenomenon of these two species or of the less homogeneous culture conditions. It is true that soil biologists have been slow to experiment with concepts of patchy environments stabilizing either competitive relationships or predator–prey interactions (Murdoch 1977; Hastings 1977); this seems a fruitful field for future research.

DISCUSSION

Attempts at understanding the structure of soil arthropod communities have been relatively unsuccessful. The review of approaches broadly grouped as 'divisive', which aimed at sampling the community and thereby unravelling the role of each species, has indicated that they have generally proved unsatisfactory. This could be because the approach does not deal in sufficient detail with the role of the individual species; it could be because it is like a 'black box' in which the results of interactions are seen but the nature of the interaction is unknown; it could be because the experimental (as opposed to sampling) and analytical techniques are not yet sufficiently developed; or it could be because the nature of the community does not allow for valid hypotheses to be made and drawn. The problem is essentially statistical in nature; efficient sampling and experimental designs might help to provide more interpretable data. More concentration on the methodology of multivariate analysis, to overcome the problem of relatively weak correlation in field data, might yield results. The factor analysis model, including as it does k common factors as well as unique or residual variances, might give an approximation to niches in k-dimensional space. The availability of factor analysis models that are not linear, although not developed from a computational point of view, may prove attractive to ecologists.

Similarly, the 'agglomerative' approaches, aiming to predict ecosystem behaviour from single-species studies and pairwise interactions, have proved

unsatisfactory because the interactions of three species together cannot be predicted from a knowledge of all the pairwise interactions; experiments indicate that 'the whole is more than the sum of the parts'. If this proves to be the general rule, it is obvious that the agglomerative approach has no future as a technique in community ecology, though it is essential for population ecology. Associated with the agglomerative approach are both statistical design and model building; the criterion for a successful experiment is the construction of a model that predicts accurately the outcome of the next experiment.

Neither the divisive nor the agglomerative approach is particularly useful in understanding the diversity of the community. Both approaches will inevitably fix on the more abundant species, and produce data on them. It is unlikely that sampling techniques will be suitable for estimating population parameters of both the abundant and the rare species, though one set of samples is used to do both tasks. No-one has yet used a sampling scheme which aims to sample the rare species of the soil fauna (usually more than half the total number of species) efficiently. Similarly, the acquisition of living material of the rare species in sufficient quantity is a difficult barrier to overcome before attempting to study their population parameters in the laboratory.

The realism of any study has also to be considered. Divisive approaches are usually working with field communities, and hence the question does not arise, though the sampling periods may be atypical (drought, colder than average, etc.) unless the period extends over several years. Laboratory studies have all been done in exceptionally homogeneous environments, none of which approaches field conditions. The effects of environmental heterogeneity need to be known if the results of laboratory studies are ever to be applied to field communities.

If neither the divisive nor the agglomerative approaches are satisfactory, what are to be used in their place? Five possibilities can be suggested.

First, no-one has sampled a community in the field whilst, at the same time, designing experiments with small numbers of species from the same community in the laboratory. Only when both approaches are tried on the same community will one know by how much they fail to satisfy the criteria of understanding the structure and functioning of the complete community.

Secondly, it would seem appropriate to attempt a combined divisive/agglomerative approach on a simple soil arthropod community, such as those of the Antarctic and sub-Antarctic (see, for example, Tilbrook 1973), where there is a chance that all species of arthropods can be encompassed both by the field sampling and by the laboratory population studies. A community of such low diversity thus has the advantage that both approaches might meet, but it has the disadvantage that results are probably not generally applicable to more diverse communities.

Thirdly, a greater knowledge of the trophic structure of the arthropod communities is required. Anderson (1975) lists some of the studies on feeding

habits of soil animals, and he comments upon the apparent predominance of generalized feeding. In some instances food webs have been constructed, but the detail is usually insufficient for the studies of community dynamics. The recent use of radioactive traces, ^{14}C by Gifford (1967), ^{32}P by Ernsting & Joosse (1974) and ^{45}Ca by Kowal & Crossley (1971), provides means whereby the connections in the food web can be identified, and possibly whereby the flow of energy and nutrients quantified. Whether such studies will agree with Anderson's statement about generality of feeding (i.e. a high degree of connectivity) or whether they demonstrate that connectivity is less than we currently think (as indicated by the studies of Mills & Sinha 1971 and Visser & Whittaker 1977) remains to be seen.

Fourthly, the study of soil communities that are not in a steady state might indicate community phenomena that were previously unknown or unsuspected. Thus, the study of a community undergoing successional change may demonstrate the characteristics of species involved in invasion and extinction processes (e.g. Parr 1978).

And finally, perturbation experiments will demonstrate how the remaining species in a community react to a major disturbance. Such experiments have frequently been tried, especially by the application of insecticides. However, the majority of these studies have recorded only the number of 'mites', 'Collembola', etc., on treated and control plots, and do not identify the groups to specific level. Other perturbations, such as mowing, raking, grazing of different intensities, silvicultural practices, the addition or subtraction of litter or the application of fungicides, have been tried, but the majority of papers in this field do not record organisms at the species level.

Amongst these observational and experimental approaches to the community, it seems essential to include the parallel development of ecological theory. The problems of whether complexity begets or reflects stability, and the effect of a perturbing factor (Goh 1975), as happens with the periodic litter fall on top of the soil arthropod community, have relevance to understanding the structure of micro-arthropod communities. It is possible that the more stable soil environment and the less complex soil arthropod community have contributed to the biological stability shown in Figure 17.2.

ACKNOWLEDGMENTS

REFERENCES

Anderson J.M. (1971) Observations on the vertical distribution of Oribatei (Acarina) in two woodland soils. *IV Colloquium Pedobiologiae* (Ed. by INRA) pp. 257–272. Proceedings of the 4th International Colloquium of Soil Zoology, Paris, 1970.

Anderson J.M. (1975) The enigma of soil animal species diversity. *Progress in Soil Zoology* pp. 51–58. Proceedings of the 5th International Colloquium of Soil Zoology, Prague, 1973. Academic, Czechoslovak Academy of Sciences.

Athias F. (1975) Donnée complémentaires sur l'abondance et la distribution verticale des microarthropodes de la savane de Lamto (Côte d'Ivoire). *Bulletin du Muséum National d'Histoire Naturelle, Écologie Générale*, **24**, 1–28.

Butcher J.W., Snider R. & Snider R.J. (1971) Bioecology of edaphic Collembola and Acarina. *Annual Review of Entomology*, **16**, 249–288.

Christiansen K. (1964) Bionomics of Collembola. *Annual Review of Entomology*, **9**, 147–178.

Christiansen K. (1967) Competition between collembolan species in culture jars. *Revue d'Écologie et de Biologie du Sol*, **4**, 439–462.

Christiansen K. (1971) Factors affecting predation on Collembola by various arthropods. *Annales de Spéléologie*, **26**, 97–106.

Costigan P.A. (1975) Experimental and computer studies on the response to exploitation of laboratory populations of *Onychiurus quadriocellatus* (Insecta: Collembola). *Unpublished B.A. thesis, University of York.*

Culver D. (1974) Competition between Collembola in a patchy environment. *Revue d'Écologie et de Biologie du Sol*, **11**, 533–540.

Curry J.P. (1973) The arthropods associated with the decomposition of some common grass and weed species in the soil. *Soil Biology and Biochemistry*, **5**, 645–657.

Curry J.P. (1976) The arthropod communities of some common grasses and weeds of pasture. *Proceedings of the Royal Irish Academy, Series B*, **76**, 641–665.

Davis P.R. (1978) Approaches towards modelling competition and predation in a simple community of soil arthropods. *Unpublished D.Phil. thesis, University of York.*

Drift J. van der (1959) Field studies on the surface fauna of forests. *Bijdragen tot de Dierkunde*, **29**, 79–103.

Emlen J.M. (1973) *Ecology: An Evolutionary Approach.* Addison-Wesley, Reading, Massachusetts.

Ernsting G. (1977) Effects of food deprivation and type of prey on predation by *Notiophilus biguttatus* F. (Carabidae) on springtails (Collembola). *Oecologia (Berlin)*, **31**, 13–20.

Ernsting G. & Joosse E.N.G. (1974) Predation on two species of surface dwelling Collembola: a study with radio-isotope labelled prey. *Pedobiologia*, **14**, 222–231.

Ghilarov M.S. (1977) Why so many species and so many individuals can coexist in the soil. *Ecological Bulletins (Stockholm)*, **25**, 593–597.

Gifford D.R. (1967) An attempt to use ^{14}C as a tracer in a Scots pine (*Pinus sylvestris* L.) litter decomposition study. *Secondary Productivity of Terrestrial Ecosystems* (Ed. by K. Petrusewicz) pp. 687–693. Panstwowe Wydawnictwo Naukowe, Warsaw & Krakow.

Gisin H. (1960) *Collembolenfauna Europas.* Museum d'Histoire Naturelle, Geneva.

Goh B.S. (1975) Stability, vulnerability and persistence of complex ecosystems. *Ecological Modelling*, **1**, 105–116.

Green C.D. (1964) The effect of crowding upon the fecundity of *Folsomia candida* (William) var. *distincta* (Bagnall) (Collembola). *Entomologia Experimentalis et Applicata*, **7**, 62–70.

Haarløv N. (1960) Microarthropods from Danish soils: ecology, phenology. *Oikos, Supplement No.* 3, 1–176.

Hale W.G. (1966) A population study of moorland Collembola. *Pedobiologia*, 6, 65–99.

Hale W.G. (1967) Collembola. *Soil Biology* (Ed. by A. Burges & F. Raw) pp. 397–411. Academic Press, London.

Harris J.R.W. (1974a) The kinetics of polyphagy. *Ecological Stability* (Ed. by M.B. Usher & M.H. Williamson) pp. 123–139. Chapman & Hall, London.

Harris J.R.W. (1974b) Aspects of the kinetics of predation with reference to a soil mite, *Pergamasus longicornis* Berlese. *Unpublished D.Phil. thesis, University of York.*

Harris J.R.W. & Usher M.B. (1978) Laboratory studies of predation by the grassland mite *Pergamasus longicornis* Berlese and their possible implications for the dynamics of populations of Collembola. *Scientific Proceedings of the Royal Dublin Society, Series A*, 6, 143–153.

Hartenstein R. (1961) On the distribution of forest soil microarthropods and their fit to 'contagious' distribution functions. *Ecology*, 42, 190–194.

Hastings A. (1977) Spatial heterogeneity and the stability of predator–prey systems. *Theoretical Population Biology*, 12, 37–48.

Huffaker C.B. (1958) Experimental studies on predation: dispersion factors and predator–prey oscillations. *Hilgardia*, 27, 343–383.

Huffaker C.B., Vrie M. van de & McMurtry J.A. (1969) The ecology of tetranychid mites and their natural control. *Annual Review of Entomology*, 14, 125–174.

Hurlbutt H.W. (1964) Structure and distribution of *Veigaia* (Mesostigmata) in forest soils. *Acarologia (1st International Congress of Acarology)*, 150–152.

Hurlbutt H.W. (1968) Coexistence and anatomical similarity in two genera of mites, *Veigaia* and *Asca*. *Systematic Zoology*, 17, 261–271.

Hutchinson G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposium in Quantitative Biology*, 22, 425–427.

Joosse E.N.G. (1969) Population structure of some surface dwelling Collembola in a coniferous forest soil. *Netherlands Journal of Zoology*, 19, 621–634.

Joosse E.N.G. (1970) The formation and biological significance of aggregations in the distribution of Collembola. *Netherlands Journal of Zoology*, 20, 299–314.

Joosse E.N.G. & Verhoef H.A. (1974) On the aggregational habits of surface dwelling Collembola. *Pedobiologia*, 14, 245–249.

Kowal N.E. & Crossley D.A. (1971) The ingestion rates of micro-arthropods in pine mor, estimated with radioactive calcium. *Ecology*, 52, 444–452.

Lawlor L.R. & Maynard Smith J. (1976) The coevolution and stability of competing species. *American Naturalist*, 110, 79–99.

Lebrun Ph. (1970) Écologie et biologie de *Nothrus palustris* (C.L. Koch 1839)—Acarien, Oribate. IV. Survivance, fécondité, action d'un prédateur. *Acarologia*, 12, 827–848.

Lions J.C. (1973) Application du concept de la diversité spécifique à la dynamique de trois populations d'oribates (acariens) de la forêt de la Sainte-Baume (Var). *Écologie Méditerranea*, 1, 165–192.

Longstaff B.C. (1974) Experimental and computer studies of competition in soil Collembola. *Unpublished D.Phil. thesis, University of York.*

Longstaff B.C. (1976) The dynamics of collembolan populations: competitive relationships in an experimental system. *Canadian Journal of Zoology*, 54, 948–962.

Longstaff B.C. (1977) The dynamics of collembolan populations: a matrix model of single species population growth. *Canadian Journal of Zoology*, 55, 314–324.

MacArthur R.H. & Pianka E.R. (1966) On optimal use of a patchy environment. *American Naturalist*, 100, 603–609.

MacArthur R.H. & Levins R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist*, **101**, 377–385.

Macfadyen A. (1952) The small arthropods of a *Molinia* fen at Cothill. *Journal of Animal Ecology*, **21**, 87–117.

Maxwell A.E. (1977) *Multivariate Analysis in Behavioural Research*. Chapman & Hall, London.

Mills J.T. & Sinha R.N. (1971) Interactions between a springtail, *Hypogastrura tullbergi*, and soil-borne fungi. *Journal of Economic Entomology*, **64**, 398–401.

Miracle M.R. (1974) Niche structure in freshwater zooplankton: a principal components approach. *Ecology*, **55**, 1306–1316.

Moritz M. (1963) Über Oribatidengemeinschaften (Acari: Oribatei) norddeutscher Laubwaldböden, unter besonderer Berücksichtigung der die Verteilung regelnden Milieubedingungen. *Pedobiologia*, **3**, 142–243.

Morris M.G. (1969) Differences between invertebrate faunas of grazed and ungrazed chalk grassland. III. The heteropterous fauna. *Journal of Applied Ecology*, **6**, 475–487.

Morris M.G. (1971) Differences between invertebrate faunas of grazed and ungrazed chalk grassland. IV. Abundance and diversity of Homoptera-Auchenorhyncha. *Journal of Applied Ecology*, **8**, 37–52.

Murdoch W.W. (1977) Stabilizing effects of spatial heterogeneity in predator–prey systems. *Theoretical Population Biology*, **11**, 252–273.

Niijima K. (1971) Seasonal changes in collembolan populations in a warm temperate forest of Japan. *Pedobiologia*, **11**, 11–26.

Pande Y.D. & Berthet P. (1975) Observations on the vertical distribution of soil Oribatei in a woodland soil. *Transactions of the Royal Entomological Society of London*, **127**, 259–275.

Parr T.W. (1978) An analysis of soil micro-arthropod succession. *Scientific Proceedings of the Royal Dublin Society, Series A*, **6**, 185–196.

Poole T.B. (1961) An ecological study of the Collembola in a coniferous forest soil. *Pedobiologia*, **1**, 113–137.

Strebel O. (1932) Beiträge zur Biologie, Ökologie und Physiologie einheimischer Collembolen. *Zeitschrift für Morphologie und Ökologie der Tiere*, **25**, 31–153.

Tamura H. (1976) Population studies on *Folsomia octoculata* (Collembola: Isotomidae) in a subalpine coniferous forest. *Revue d'Écologie et de Biologie du Sol*, **13**, 69–91.

Tilbrook P.J. (1973) The signy Island terrestrial reference sites. I. An introduction. *British Antarctic Survey Bulletin*, **33 & 34**, 65–76.

Usher M.B. (1969) Some properties of the aggregations of soil arthropods: Collembola. *Journal of Animal Ecology*, **38**, 607–622.

Usher M.B. (1970) Seasonal and vertical distribution of a population of soil arthropods: Collembola. *Pedobiologia*, **10**, 224–236.

Usher M.B. (1971a) Properties of the aggregations of soil arthropods, particularly Mesostigmata (Acarina). *Oikos*, **22**, 43–49.

Usher M.B. (1971b) Seasonal and vertical distribution of a population of soil arthropods: Mesostigmata. *Pedobiologia*, **11**, 27–39.

Usher M.B. (1975a) Some properties of the aggregations of soil arthropods: Cryptostigmata. *Pedobiologia*, **15**, 355–363.

Usher M.B. (1975b) Seasonal and vertical distribution of a population of soil arthropods: Cryptostigmata. *Pedobiologia*, **15**, 364–374.

Usher M.B. (1976) Aggregation responses of soil arthropods in relation to the soil environment. *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes* (Ed. by J.M. Anderson & A. Macfadyen) pp. 61–94. Blackwell Scientific Publications, Oxford.

Usher M.B. & Balogun R.A. (1966) A defence mechanism in *Onychiurus* (Collembola, Onychiuridae). *Entomologists' Monthly Magazine*, **102**, 237–238.

Usher M.B., Longstaff B.C. & Southall D.R. (1971) Studies on populations of *Folsomia candida* (Insecta: Collembola). The productivity of populations in relation to food and exploitation. *Oecologia (Berlin)*, **7**, 68–79.

Usher M.B. & Stoneman C.F. (1977) *Folsomia candida*—an ideal organism for population studies in the laboratory. *Journal of Biological Education*, **11**, 83–90.

Verhoef H.A., Nagelkerke C.J. & Joosse E.N.G. (1977) Aggregation pheromones in Collembola (Apterygota): a biotic cause of aggregation. *Revue d'Écologie et de Biologie du Sol*, **14**, 21–25.

Visser S. & Whittaker J.B. (1977) Feeding preference of certain litter fungi by *Onychiurus subtenuis* (Collembola). *Oikos*, **29**, 320–325.

Waldorf E. (1971a) Selective egg cannibalism in *Sinella curviseta* (Collembola: Entomobryidae). *Ecology*, **52**, 673–675.

Waldorf E.S. (1971b) Oviposition inhibition in *Sinella curviseta* (Collembola: Entomobryidae). *Transactions of the American Microscopical Society*, **90**, 314–325.

Wallace M.M.H. (1967) The ecology of *Sminthurus viridis* (L.) (Collembola). I. Processes influencing numbers in pastures in Western Australia. *Australian Journal of Zoology*, **15**, 1173–1206.

Wallwork J.A. (1967) Acari. *Soil Biology* (Ed. by A. Burges & F. Raw) pp. 363–395. Academic Press, London.

Wood T.G. (1967) Acari and Collembola of moorland soils from Yorkshire, England. I. Description of the sites and their populations. *Oikos*, **18**, 102–117.